Anomalocaris**:** the largest Cambrian predator.
A specimen of *Anomalocaris* collected from the Burgess Shale by the Royal Ontario Museum in 1991 with the new reconstruction by Quade Paul, showing the anterior appendages, which were used for capturing prey. *Anomalocaris*, like *Opabinia*, was a stem arthropod. (Photograph: with permission from Roberts & Company Publishers; reconstruction: ©Quade Paul).

appeared, predator-prey interactions resulted in more selection pressure. Exceptionally preserved fossil occurrences reveal an increase in ecological complexity over time. Escalation in the number of different modes of life includes the exploitation of a greater range of levels above and below the sediment surface (tiering), as well as diversification of feeding mechanisms and modes of locomotion. This can be illustrated as the progressive filling of a three-dimensional grid with modes of tiering, feeding and mobility (attached or mobile) on each axis, depicted like an exploded multielement Rubik's Cube. Occupancy of potential modes of life (blocks in the grid) increases dramatically from Ediacaran to Cambrian times. Similar interpretations of modes of life have been used to reconstruct food webs (reminiscent of an inverted bird's nest) for the older Chengjiang and the younger Burgess Shale faunas. These clearly show that ecological complexity increased in the Cambrian. To a significant degree, it was the organisms themselves that drove ecological and therefore evolutionary change. Where this involves animals altering their environment it can be described as ecological engineering — Erwin and Valentine argue, for example, that an increase in burrowing organisms resulted in oxygenation of sediment and increased productivity, and had a strong positive feedback on population sizes and even biodiversity. Such fundamental ecological innovations may explain the explosion of morphological diversity in the Cambrian.

The fossils provide evidence of what happened and when, although small size and low preservation potential conceal the earliest evolution of major groups. Future research on the fossil record will reveal more of the environmental setting of the explosion and how it was affected by ecological engineering. But as Erwin and Valentine explain, the final piece of the puzzle, the explanation for the rapid appearance of such a range of different animals, comes from a new understanding of genetic controls of development. Comparisons of such controls in different animal groups reveals the sequence in which developmental processes evolved in metazoans. Such regulatory interactions can be visualized as complex networks, reminiscent of wiring diagrams. The major attributes of phyla are determined by the highly conserved arrangement in the core or kernel of these networks; more flexible links around the periphery of the network determine the nature of species. The Cambrian explosion provided the foundation of life in the world's oceans today. Erwin and Valentine's book is the first to explore in detail the influence of both genomic and ecological agents in driving the diversification of major groups during the Cambrian explosion. This active area of research will refine our understanding of why the explosion occurred when it did. As the authors conclude (p. 342): "*there can hardly be more of a challenge [...] than to describe and interpret the confluence of history and process responsible for events during that remote and critical time in life's history.*"

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Q & A

Denis Pelli

Denis G. Pelli studied Applied Math at Harvard ('75) and then did a PhD in Visual Physiology, on "Effects of visual noise", at Cambridge University with Fergus Campbell and John Robson ('81). He did a postdoc with Gordon Legge on the visual requirements of reading at the University of Minnesota, and then joined the faculty of the Institute for Sensory Research at Syracuse University. Since 1995, he has been Professor of Psychology and Neural Science at New York University. During the Michaelmas terms of 2011 and 2012, he was a Visiting Fellow Commoner at Trinity College, Cambridge, working with Horace Barlow on a psychophysical method for counting the cortical neurons used in a perceptual task. Most of Pelli's work is psychophysical, measuring perceptual thresholds to discover how object recognition works. He has championed the use of masking by visual noise and of crowding by clutter. In masking, the target becomes invisible, and thus unrecognizable, because an overlapping mask pattern stimulates the same feature detectors as the target does; in crowding, the target remains visible, but is unrecognizable, a jumbled mess, because vision has combined neighboring clutter with the target object. With students and collaborators, he has characterized the intrinsic noise of vision and the channel for letter identification and reading. Pelli and his colleagues have found that computational efficiency is invariant with viewing conditions but inversely proportional to complexity. He showed that, to escape crowding, the target must be separated from clutter by 6 mm in the cortical representation. The effects of complexity and crowding both suggest an early bottleneck in the transmission of information for object recognition. Pelli is a co-creator of the widely used QUEST and Psychtoolbox public-domain software, and the Pelli–Robson Contrast Sensitivity Chart. He and his former student Sarah Rosen applied for a US patent on using a gaze-contingent display to reduce crowding and increase reading speed. His Optical Society of America Leadership

Award/New Focus Prize, 2000, says, "Through leadership in visual science, Dr. Pelli has benefited artists, scholars, and the visually impaired."

What turned you on to vision in the first place? I grew up in a family of artists. My father and brother (Cesar and Rafael) are architects and my mother (Diana Balmori) is a landscape designer. For as long as I can remember, we have always talked mostly about how things look, and especially why something looks particularly good. I wanted to be an inventor, and was fascinated by machines: as an undergraduate, I invented a nine-transistor self-timer for the then-new SX-70 instant camera, and showed it to Polaroid; and I spun epoxy to make a parabolic mirror for a telescope without grinding or polishing.

After reading David Hubel's 1963 article "The Visual Cortex of the Brain" in *Scientific American*, I decided that the brain was the coolest machine around. In a vision journal club at Harvard, I read the Campbell and Robson 1968 paper on "Application of Fourier analysis to the visibility of gratings", and I was hooked. I did my PhD in John Robson's lab, supervised by Fergus Campbell. My science has occasionally touched on art: to explain the duality in Chuck Close's blocky portraits; to exploit the experience of observation provided by James Turrell's Skyspace at PS1; and using my peripheral vision research to help Julia Gleich create the part of her 2012 "Brodmann Areas" ballet that is meant to be seen out of the corner of your eye (http://denispelli.com).

What's the best advice you've been given, and what would you offer? I once asked John Robson, over breakfast at his house, when we were working on the Pelli–Robson chart, how he managed to be always right about everything. He smiled, and said that if he gives that impression it is merely because he keeps his mouth shut when he doesn't really know.

Every year, I mentor high school students doing science projects for the Intel science competition. I try to get them to view science as storytelling. First one tries to discern the story behind a phenomenon (like reading by the profoundly deaf); then one tries to tell the story so as to convince one's peers. Both parts, discerning and telling, are needed and hard, and they make science a delightful game.

What's your favorite paper? Two papers, one by Horace Barlow and one by Robson and Graham, did a lot to introduce the statistical perspective to perception research. Modern statistics arose near the beginning of the twentieth century, to analyze agricultural field trials and barley for beer. Today, we all think of vision as a statistician who's always busy testing hypotheses about the world, but no one thought that before 1900. Fechner does not mention statistics, not even standard errors. Helmholtz had the hypotheses, but not the statistics. In the early 1900s the statistical nature of quantum mechanics shocked everyone. The statistical perspective arrived to perception later, but was still wrenching. Many people contributed to the paradigm shift, but I was particularly impressed by two. In his famous 1953 paper about summation and inhibition in the frog eye, Barlow said, "The receptive field of an 'on-off' unit would be nicely filled by the image of a fly at 2 in. distance and it is difficult to avoid the conclusion that the 'on-off' units are matched to this stimulus and act as 'fly detectors'". Barlow is telling us that the neuron computes likelihood; taking the fly to be at the location of the most active neuron would be maximum likelihood estimation, introduced earlier by R.A. Fisher. In 1981, Robson and Graham tested probability summation over a large range of extents. They showed that statistical independence of feature detections makes strong behavioral predictions that transcend physiological details.

What about electronic publishing? For over a century, our societies strove to achieve universal literacy. Authorship is now catching up. Extrapolating from the historical record up to 2009, we predicted universal authorship in 2013 (or 2014) (http://seedmagazine.com/content/article/a_writing_revolution/). We considered an author's text 'published' if a hundred (or a thousand) people read it. The power of the pen, or tweeting, is becoming universal, and may soon be deemed a human right.

What is your greatest ambition? I didn't read Fechner's 1860 *Elements of Psychophysics* until the late 90s, but I owe him. I am a psychophysicist, and he coined the word 'psychophysics'. He framed psychophysics with an emphasis on measuring thresholds to understand object recognition. Most of my work has contributed to that effort, and I have the hunch that visual scientists will solve this puzzle soon, providing a computational account of object recognition and visual sensitivity. As the goal of understanding object recognition comes within reach, I have suddenly realized that it won't address my lifelong interest in understanding why some things look so good: beautiful. The channel for a letter is fairly narrow (an octave), and very likely does not see much difference among the hundreds of fonts that publishers buy to display text. Indeed, reading speed varies little among widely used fonts. On the other hand, the Dutch type designer Gerard Unger, in his 2007 book *While You're Reading,* recounts getting to page 6 of his newly arrived copy of a detective novel without noticing that he hadn't yet read a word. As a type designer, he was merely enjoying the letter shapes. Object recognition categorizes, which may be independent of experiencing beauty. So I've started a new project to identify the conditions that enable or disable the experience of beauty.

Photo: Zach Gross

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